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Article



Revision of Palaearctic and Oriental *Necrophila* Kirby & Spence, part 2: subgenus *Chrysosilpha* Portevin (Coleoptera: Silphidae)

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Abstract

A taxonomic revision of the subgenus *Chrysosilpha* Portevin, 1921 (of the genus *Necrophila* Kirby & Spence, 1828) is presented. Three valid species are recognized: (1) *N*. (*C*.) *formosa* (Laporte, 1832), comb. nov. (ex *Silpha* Linnaeus, 1758), widely distributed from Laos and Vietnam through the Malay Peninsula, to Sumatra and Bali, with *Silpha chloroptera* Laporte, 1840 and *Chrysosilpha chloroptera* var. *magnifica* Portevin, 1921 as newly established junior subjective synonyms; (2) *N*. (*C*.) *renatae* (Portevin, 1920), comb. nov. (ex *Silpha*), endemic to Sulawesi; and (3) *N*. (*C*.) *viridis* (Motschulsky, 1861), comb. nov. (ex *Oiceoptoma* Leach, 1815), endemic to the Philippines. Lectotypes are designated for *Silpha formosa* Laporte, 1832; *Silpha chloroptera* Laporte, 1840 and *Chrysosilpha chloroptera* var. *magnifica* Portevin, 1921. Georeferenced records for all three species are mapped. Parsimony analysis supports the monophyly of *Chrysosilpha*, with *N*. (*C*.) *formosa* as the sister to a clade of *N*. (*C*.) *renatae* and *N*. (*C*.) *viridis*. Geometrical morphometrics (thin-plate spline) discriminated the three species of *Chrysosilpha*; the first two relative warp axes indicated 70.31% shape variation in males and 77.18% in females, which was further confirmed by MANOVA to be highly significant. Canonical variate analysis indicated no overlap between the three taxa and enabled a 100% correct classification of each specimen to its group mean.

Key words: taxonomy, new synonymy, new combination, phylogeny, geometric morphometrics, distribution, Oriental region, Wallacea

Introduction

Portevin (1921) erected *Chrysosilpha* as a separate genus, close to *Calosilpha* Portevin, 1920 (described by Portevin 1920a), to accommodate five species of carrion beetles with colorful adults: *Chrysosilpha formosa* (Laporte, 1832), *C. chloroptera* (Laporte, 1840), *C. renatae* (Portevin, 1920), *C. viridis* (Motschulsky, 1861) and *C. coelestis* (Dohrn, 1875), all from the Oriental region. In the same paper, he also described *C. chloroptera* var. *magnifica*, based on minor differences in shine of the elytral surface (Portevin 1921). Portevin (1926) redescribed the genus, and provided a detailed key and a catalogue. However, *Silpha formosa* Laporte, 1832 was designated as the type species of *Chrysosilpha* only subsequently by Hatch (1928), who also treated *Chrysosilpha* as a subgenus of *Silpha* Linnaeus, 1758. Later, Arnett (1950) treated the only species of this clade from the Philippines as *Oiceoptoma (Thanatophilus) viridis*. Only recently, Peck (2001) and Sikes (2008) listed *Chrysosilpha* along with *Calosilpha, Deutosilpha* Portevin, 1920 and *Eusilpha* Semenov, 1890 as subgenera of *Necrophila* Kirby & Spence, 1828, following an unpublished taxonomic revision by A.F. Newton, Jr. This classification is also followed here, and detailed phylogenetic relationships of all subgenera will be treated in a separate study (J. Růžička, unpublished).

Recently, Ikeda *et al.* (2008) published a phylogenetic reconstruction of the Silphinae based on sequences of one mitochondrial gene (16S) and three nuclear genes (28S, wingless (Wg), and phosphoenolpyruvate carboxykinase (PepCK)). Both Bayesian analysis and maximum parsimony produced the following tree topology: *Necrophila* + (*Eusilpha* + (*Calosilpha* + *Chrysosilpha*)) (Ikeda *et al.* 2008: 2072, fig. 1).

The aim of this paper is to redescribe the subgenus *Necrophila* (*Chrysosilpha*), distributed in the Oriental region and Wallacea. Only three species are herein considered valid, and are newly combined as belonging to *Necrophila* (*Chrysosilpha*). The detailed distribution of the species is summarized and mapped, based on the examination of 518 specimens from 26 museum or private collections. Adult seasonal activity is also summarized, based on the examined specimens.

We also employed geometric morphometrics, one of the most influential and frequently used techniques to find variation in shape within and among species (Bookstein 1991, Zelditch *et al.* 2004). Its value for taxonomic studies is irrefutable, as it assists in the validation of synonyms and in determining new species and subspecies (for applications in taxonomy of beetles, see Pretorius & Scholtz 2001, Roggero 2004, or Hájek & Fikáček 2010).

Here, we apply this technique to distinguish and demonstrate the shape differences of the elytral apex among the taxa of *Chrysosilpha* and their sexes in order to further test our taxonomic and phylogenetic findings.

Material and methods

Museum abbreviations. Specimens examined in this study are deposited in the following museums and private collections (acronyms according to Arnett *et al.* 1993):

BMNH	Natural History Museum, London, United Kingdom (M.V.L. Barclay);
FMNH	Field Museum of Natural History, Chicago, U.S.A. (A.F. Newton, J.H. Boone);
HNHM	Magyar Természettudományi Muzeum, Budapest, Hungary (O. Merkl);
IRSNB	Institut royal des Sciences naturelles de Belgique, Belgium, Brussels (D. Drugmand, Martina
	Peeters);
JRUC	collection of Jan Růžička, Praha, Czech Republic;
JSCC	collection of Jan Schneider, Praha, Czech Republic;
LKLC	collection of Libor Klíma, Ostrava, Czech Republic;
MHNG	Muséum d'Histoire Naturelle, Genève, Switzerland (G. Cuccodoro);
MNHN	Muséum national d'Histoire naturelle, Paris, France (†Nicole Berti, Azadeh Taghavian);
MNIC	collection of M. Nishikawa, Ebina, Japan;
NHMB	Naturhistorisches Museum, Basel, Switzerland (M. Brancucci);
NHMW	Naturhistorisches Museum, Wien, Austria (H. Schönmann, H. Schillhammer);
NHRS	Naturhistoriska riksmuseet, Stockholm, Sweden (B. Viklund);
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, U.S.A. (D. Furth, G.F.
	Hevel);
NSMT	National Science Museum, Tokyo, Japan (S. Nomura);
OUMNH	Oxford University Museum of Natural History, Oxford, United Kingdom (J. Hogan, D.J. Mann);
RMNH	Netherlands Centre for Biodiversity Naturalis, Leiden, the Netherlands (Eulalia Gasso Miracle, A.
	von Assen);
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (L. Zerche);
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany (W. Schawaller);
SMTD	Staatliches Museum für Tierkunde, Dresden, Germany (O. Jäger);
TFUC	collection of T. Fukuzawa, Kanagawa, Japan;
WBAC	collection of W. Barries, Wien, Austria;
ZMAN	Zoölogisch Museum Amsterdam, Amsterdam, the Netherlands (S.A. Ulenberg, W. Hogenes);
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen, Denmark (A.Yu. Solodovnikov);
ZMUM	Zoological Museum of Moscow Lomonosov State University, Moscow, Russia (N. Nikitsky);
ZSM	Zoologische Staatssammlung, München, Germany (M. Balke).

Morphological analyses. Photographs of habitus and morphological details were taken using an Olympus SZX10 stereomicroscope with Olympus E-330 camera attached or with a Canon macro photo lens MP-E 65mm or EF-S 60mm on a Canon 550D and multiple (28–110) layers of focus combined in the Zerene Stacker 1.04 software (Zerene Systems 2011; http://www.zerenesystems.com/cms/stacker).

Male and female terminalia were studied after short clearing in hot 10% solution of KOH, mounted in temporary glycerine mounts for line drawings. General morphological terms used follow Lawrence *et al.* (2010), while terminology for male genital segment follows mostly Blackburn (1936).

Exact label data are cited only for the type material. Separate lines on labels are indicated (only for primary types) by "/", separate labels by "//". Author's remarks and comments are enclosed in square brackets: [p] – preceding data are printed; [hw] – preceding data are hand-written.

Microsoft Encarta Premium 2008 (Microsoft Corporation 2007), NGA GEOnet Names Server (National Geospatial-Intelligence Agency 2011; http://earth-info.nga.mil/gns/html/index.html), Google Earth (Google 2011; http://earth.google.com) and Fuzzy Gazetteer (C. Kohlschütter 2011; http://isodp.fh-hof.de/fuzzyg/query/) were used to find coordinates for most of the localities. The distribution map was produced and edited in ESRI ArcMap 9.3 of ArcGIS Desktop 9.3 suite. For map layers, free level 0 and level 1 data from Global Administrative Areas (http://www.gadm.org/world) were used.

Phylogenetic analysis. Phylogenetic analysis was performed using a matrix (Table 1) comprising three terminal taxa of the ingroup and 19 characters (15 of which are parsimony informative characters) for external adult morphology. The matrix was compiled in Winclada version 1.00.08 (Nixon 2002), and analysed by exhaustive search ("implicit enumeration" option) using TNT ver. 1.1 (Goloboff *et al.* 2008). All characters were equally weighted and multi-state characters were treated as unordered. Standard bootstrap analysis (with 1000 replicates) was executed in TNT; tree visualization and character mapping were done in Winclada.

Necrophila (Eusilpha) japonica (Motschulsky, 1861) (Motschulsky 1861b), a type species of *Eusilpha*, and *N*. (*Necrophila) americana* (Linnaeus, 1758), a type species of *Necrophila*, were selected as outgroups, because these subgenera were hypothesized to be sister groups to *Calosilpha* and *Chrysosilpha* in the recent phylogenetic reconstruction of Ikeda *et al.* (2008). The character scoring was based on the following material: *N.* (*N.*) *americana*: Canada, Ontario, Point Pelee, vi.1995, D. Čatloš leg., 2 $\Im \Im$ (JRUC); U.S.A., Minnesota, Sherburne Co., Sherburne Wildlife Refuge, 28.vi.1990, 1 \bigcirc (JRUC); Canada, Quebec, Wakefield, 11.vi.1989, Hutchinson leg., 1 \bigcirc (JRUC); *N.* (*E.*) *japonica*: Japan, Kyushu, Fukuoka prefecture, Motooka, 7.–10.vii.1994, S. Nomura leg., pitfall traps, 1 \Im , 1 \bigcirc (JRUC).

Character list

- 1. Frons in dorsal view: (0) without fovea or with weakly indicated fovea between the eyes (Fig. 29; Blackburn 1936: fig. 1); (1) with distinctly indicated fovea (Figs. 30, 31).
- 2. Anterior emargination of labrum: (0) narrow, deep (Figs. 29, 30; Blackburn 1936: fig. 5); (1) wide, shallow (Fig. 31).
- 3. Punctation of pronotum in dorsal view: (0) uniform; (1) very superficial discally, arranged in four parallel patches (Figs. 25–28).
- 4. Shape of pronotal punctures in dorsal view: (0) simple, round to oval (Figs. 25–28); (1) modified, horseshoe-shaped (Fig. 32).
- Colour of pronotum in dorsal view: (0) yellow with black disc (Blackburn 1936: fig. 1); (1) black; (2) orange with four large spots (Figs. 1–2); (3) metallic blue or green-blue with anterolateral or lateral part orange (Figs. 3–6).
- 6. Proventrite colouration: (0) black; (1) metallic blue or green (Fig. 34); (2) orange, with metallic blue only on medial projection (Fig. 33).
- Punctation of scutellum: (0) large (distance between punctures is 0.2–0.5 times the diameter of one puncture);
 (1) fine to very fine (distance between punctures is 1–5 times the diameter of one puncture).
- 8. Surface of elytron: (0) unmodified (Fig. 1–6); (1) with reticulate sculpturing (Blackburn 1936: fig. 1).
- 9. Colour of elytra in dorsal view: (0) black; (1) metallic blue or green (Fig. 1–6).
- 10. Elytral epipleural ridge, lateral elevation in dorsal view: (0) flat (Blackburn 1936: fig. 1); (1) weakly elevated (Figs. 1–6).
- 11. Elytral epipleural ridge, setation dorsally in females: (0) bare; (1) with dense setation.
- 12. Elytral epipleura, ventral view in males: (0) simple (Blackburn 1936: fig. 2); (1) with a prominent, oblique crest posteriorly (Fig. 37).
- 13. Apex of elytron, male: (0) regularly rounded (Fig. 1); (1) truncate (Figs. 3, 5).

- 14. Apex of elytron, female: (0) simple (Fig. 2); (1) with suture extended into larger, acute denticle (Figs. 4, 6).
- 15. Male genital segment, spiculum gastrale, thickness: (0) robust (Fig. 8; Blackburn 1936: fig. 39); (1) slender (Figs. 12, 16).
- 16. Male genital segment, shape of ventrite 9: (0) short, constricted anteriorly (Blackburn 1936: fig. 39); (1) elongate, constricted anteriorly; (2) elongate, oval (Figs. 8, 12, 16).
- 17. Male aedeagus, lateral part of basal portion in ventral view: (0) slender (Figs. 11, 15; Blackburn 1936: fig. 39); (1) robust (Fig. 7).
- 18. Male aedeagus, median lobe in ventral view: (0) very slender (Fig. 15; Blackburn 1936: fig. 39); (1) slender (Fig. 11); robust (Fig. 7).
- 19. Female stylus length in ventral view: (0) distinctly longer than apex of coxite (Figs. 10, 14; Blackburn 1936: fig. 45); (1) as long as or only slightly longer than apex of coxite (Fig. 18).

TABLE 1. Data matrix of adult morphological characters for phylogenetic analysis of the Oriental species of *Necrophila* (*Chrysosilpha*).

species/character	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
N. (N.) americana (outgroup)	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
N. (E.) japonica (outgroup)		0	1	0	1	0	0	0	0	0	1	0	0	1	1	1	0	2	1
N. (C.) formosa	1	0	1	0	2	2	1	0	1	1	0	1	0	0	0	2	1	2	0
N. (C.) renatae	1	1	1	0	3	1	1	0	1	1	0	1	1	1	1	2	0	1	0
N. (C.) viridis	1	1	1	0	3	1	1	0	1	1	0	1	1	1	1	2	0	0	1

Geometric morphometrics. Three taxa of the subgenus *Chrysosilpha* were investigated: *N*. (*C*.) *formosa* (47 $\Diamond \Diamond$, 56 $\bigcirc \bigcirc$), *N*. (*C*.) *renatae* (20 $\Diamond \Diamond$, 23 $\bigcirc \bigcirc$) and *N*. (*C*.) *viridis* (51 $\Diamond \Diamond$, 44 $\bigcirc \bigcirc$). Images of adults in dorsal view were captured by Olympus digital reflex camera (model E-330) connected to Olympus SZX10 stereomicroscope.

The thin-plate spline (TPS) package, free software that is available at http://life.bio.sunysb.edu/morph/ index.html (Rohlf 2011), was used in the geometric morphometrics analysis. The theory behind this technique is based on coordinates of specific locations called landmarks that are precise points on each sample studied (Bookstein 1982, 1986, 1989 and 1991) and represent the specimen's morphology.

A curve, generated by the "draw background curves" module, outlining the apex of the left elytron formed from 50 points, was digitized using TpsDig 2.10 (Rohlf 2006), taking into consideration the homology of these points on all samples and their reliability in demonstrating the highest shape variability. Subsequently, the curve points were converted into landmarks using TpsUtil 1.44 (Rohlf 2009).

TpsRelw 1.49 (Rohlf 2010) was employed to display the shape variation among the specimens. Landmarks were superimposed by generalized Procrustes analysis; corresponding (homologous) landmarks were arranged over each other in a way that they would be as close to one another as possible by moving, scaling (enlarging or minimizing) and rotating them without changing their overall shape (Rohlf 1990, Rohlf & Slice 1990, Rohlf & Marcus 1993). The program performs the relative warp analysis where relative warps are used to describe the shape dissimilarity and visualize it using D'Arcy Thompson's transformation grids. The deformations in the grids represent the shape changes (Rohlf 1993, Richtsmeier *et al.* 2002, Adams *et al.* 2004, Zelditch *et al.* 2004).

The results of the first two relative warps were subsequently plotted on an axis system and given different indication symbols. This was produced by PAST ver. 2.11; free program at http://folk.uio.no/ohammer/past/ (Hammer *et al.* 2011).

Multivariate analysis of variance (MANOVA) was applied on the relative warp scores matrix to test the significance of the variations between groups (taxa/sexes), and canonical variate analysis (CVA) was performed to illustrate these differences (Zelditch *et al.* 2004). Graphical visualization of the CVA results representing the locations of the studied taxa and sexes was also demonstrated. All of the preceding analyses were executed in PAST (Hammer *et al.* 2011).

Results

Taxonomic section

Subgenus Necrophila (Chrysosilpha) Portevin, 1921

Chrysosilpha Portevin, 1921: 538 (type species *Silpha formosa* Laporte, 1832, subsequent designation by Hatch 1928: 112). *Silpha (Chrysosilpha)*: Hatch 1928: 112 (as subgenus of *Silpha*, catalogue) *Necrophila (Chrysosilpha)*: Peck 2001: 270 (as subgenus of *Necrophila*, catalogue)

Diagnostic description. Body flattened, length 12.0–18.5 mm. Body metallic blue or green (with light brown lustre in subteneral specimens), head sometimes with red brown to yellow gular region, last three antennomeres matt and black. Pronotum orange with four large spots arranged in quadrate position medially on the disc (Fig. 1–2); or, the pronotum is also metallic blue or green-blue with anterolateral or lateral part orange (Figs. 3–6, 26–28). Proventrite metallic blue or green (Fig. 34), or mostly orange, with metallic green only posteriorly on medial projection (Fig. 33).

Head flattened, with row of long erect black setae behind the eye (Figs. 30, 31). Frons with distinctly indicated fovea between the eyes, deep dorsal tentorial pits and a transverse crest posteriorly (Figs. 30, 31). Eyes large, prominently protruding from the head outline, reniform (Figs. 30, 31). Antennae with last four antennomeres forming distinct antennal club (Fig. 35).

Pronotum hexagonal in shape, with broadly rounded posterolateral corners (Figs. 25–28), anterior margin distinctly emarginate, posterior margin straight or regularly rounded (Figs. 25–28). Surface with dense punctures, larger in size posteriorly than laterally, and only very superficial discally (Figs. 25–28), without setation. Interstices between the puncures glossy, with very fine isodiametric microsculpture, sometimes only very superficial or without microsculpture discally. Anterior and posterior margin with dense row of stout, short, yellow, ventrally oriented setae.

Scutellum small, cordiform, with slightly sinuous lateral margins. Sparsely covered by fine to very fine, superficial punctures.

Elytra flattened, each elytron with three distinctly developed costae both in males and females, outer (third) costa shorter, not crossing bulges (Figs. 1–6). Elytral epipleural ridge weakly elevated in dorsal view, reaching subapical part of elytra both in males and females (Figs 1–6). Apex of elytron in males regularly rounded, or truncate with suture extended in minor apical denticle (Figs. 3, 5); in females elongated slightly or distinctly (then with suture extended into distinct, acute, larger denticle) (Figs. 2, 4, 6). Dorsal surface without reticulate sculpturing, with uniformly dispersed, fine and dense punctation, similar to that laterally on pronotum. Surface glossy, with distinct isodiametric microsculpture, slightly more coarse than on pronotum. Ventrally, elytral epipleura with larger punctures; posteriorly, in males with a prominent, oblique crest (Fig. 37, indicated by arrow), which is not developed in females.

Hind wings fully developed, functional.

Ventral side of body and legs very glossy, with fine, transverse microsculpture.

Legs with almost straight tibia (only mesotibia subsinuate), tibia armed with several longitudinal rows of short, strong setae. Pro- and mesofemur only slightly expanded distally in males and simple in females, without distinct expansion. Pro- and mesotarsomere 1–4 moderately expanded in males (simple, unmodified in females). Meso- and metatarsal claws slightly asymmetrical in males (Fig. 36), symmetrical in females.

Abdomen weakly sclerotized, with very short ventrites 2–5 (Fig. 38), connected by long, black intersegmental membranes with distinct isodiametric microsculpture (Fig. 39).

Male. Genital segment with longitudinal ventrite 9, extending anterior margin of tergum 9 (Figs. 8, 12, 16); spiculum gastrale medium to large in size, relatively slender to robust, usually slightly asymmetrical (Fig. 8, 12, 16). Aedeagus very small (length 2.8–3.0 mm), with median lobe shorter than robust parameres (Figs. 7, 11, 15).

Female. Genital segment with tergum 10 oval, subhexagonal in shape in dorsal view (Figs. 9, 13, 17). Stylus inserted laterally, slightly to distinctly longer than apex of coxite in ventral view (Figs. 10, 14, 18).

A key to species of *Necrophila* (*Chrysosilpha*)

Necrophila (Chrysosilpha) formosa (Laporte, 1832), comb. nov.

(Figs. 1–2, 7–10, 19–21, 25, 30, 33, 40)

Silpha (Oiceoptoma) Formosa Laporte, 1832: 400 (description, type locality "Siam")

Silpha formosa: Gemminger & Harold 1868: 724 (senior subjective synonym of Silpha tetraspilota Hope, 1835)

Eusilpha formosa: Portevin 1905: 51 (new combination)

Silpha formosa: Arrow 1909: 190 (new combination, *Silpha tetraspilota* Hope, 1835 removed from synonymy with *S. formosa*) *Calosilpha formosa*: Portevin 1920: 398 (new combination)

Chrysosilpha formosa: Portevin 1921: 538 (new combination, supplementary description)

Chrysosilpha formosa: Portevin 1926: 105–106, 150 (key, catalogue)

Silpha (Chrysosilpha) formosa: Hatch 1928: 112 (new combination, catalogue)

Silpha chloroptera Laporte, 1840: 5 (description with reference to Laporte 1832, type locality "Cochinchine"), syn. nov.

Eusilpha chloroptera: Portevin 1905: 51 (new combination, junior subjective synonym of Silpha formosa)

Calosilpha chloroptera: Portevin 1920a: 398 (new combination)

Chrysosilpha chloroptera Portevin, 1921: 538 (new combination, supplementary description, removed from synonymy with *Silpha formosa*)

Chrysosilpha chloroptera: Portevin, 1926: 106–107, 150 (key, catalogue)

Silpha (Chrysosilpha) chloroptera: Hatch 1928: 112 (new combination, catalogue)

Chrysosilpha chloroptera var. magnifica Portevin, 1921: 538 (type locality not specified), syn. nov.

Chrysosilpha chloroptera var. magnifica: Portevin 1926: 107, 150 (key, catalogue)

Silpha (Chrysosilpha) chloroptera var. magnifica: Hatch 1928: 112 (new combination, catalogue)

Type material examined. Lectotype \bigcirc of *Silpha formosa* (MNHN) (here designated) (only left two basal antennomeres present on left antenna), labelled (Fig. 19): "8 / 71 [hw, illegible, round label, yellow on underside] // MUSEUM PARIS [p] / Siam [hw] [= Thailand, until 1939] / MNISZECH 187 [p] 1 [hw] // TYPE [p, red label] // LECTOTYPE / Silpha (Oiceoptoma) / formosa Laporte, 1832 / Jan Růžička des. 2009 [p, red label] // Necrophila (Chrysosilpha) / formosa / (Laporte, 1832) [p] \bigcirc [hw] / Jan Růžička det. 200 [p] 8 [hw]";

Lectotype \bigcirc of *Silpha chloroptera* (MNHN) (here designated), labelled (Fig. 20): "Collection Mniszech [p] // Cochinch. [hw, Laporte's ms] [= Cochinchine, southern part of Vietnam, centroid ca. 11°00'N 107°00'E] // S. nom / chloroptera / Cast [hw, Laporte's ms] // TYPE [p, red label] // MUSEUM PARIS / COLL. A. GROUVELLE 1917 [p] // LECTOTYPE / Silpha chloroptera / Laporte, 1840 / Jan Růžička des. 2009 [p, red label] // Necrophila / (Chrysosilpha) / formosa / (Laporte, 1832) [p] \bigcirc [hw] / Jan Růžička det. 200 [p] 8 [hw]"; 1 paralectotype \eth (MNHN), labelled: "Collection Mniszech [p] // Cochinchine [hw, Laporte's ms] // TYPE [p, red label] // MUSEUM PARIS / COLL. A. GROUVELLE 1917 [p] // PARALECTOTYPE / Silpha chloroptera / Laporte, 1840 / Jan Růžička des. 2009 [p, red label] // Necrophila / (Chrysosilpha) / formosa / (Laporte, 1832) [p] \circlearrowright [hw] / Jan Růžička det. 200 [p] 8 [hw]";

Lectotype \bigcirc of *Chrysosilpha chloroptera* var. *magnifica* (MNHN) (here designated), labelled (Fig. 21): "Bedagei. int. / Sumatra's O.K. / ±600' 2^{de} Sem. [18]89, / I.Z. Kannegieter [p] // MUSEUM PARIS / COLL. A. GROUVELLE 1917 [p] // TYPE [p, red characters] // LECTOTYPE / Chrysosilpha / chloroptera var. / magnifica Portevin, 1921 / Jan Růžička des. 2009 [p, red label] // Necrophila / (Chrysosilpha) / formosa / (Laporte, 1832) [p] \bigcirc [hw] / Jan Růžička det. 200 [p] 8 [hw]"; 1 paralectotype \bigcirc (MNHN), labelled "Bedagei. int. / Sumatra's O.K. / ±600' 2^{de} Sem. [18]89 / I.Z. Kannegieter [p] // MUSEUM PARIS / COLL. A. GROUVELLE 1917 [p] // PARALECTOTYPE / Chrysosilpha / chloroptera var. / magnifica Portevin, 1921 / Jan Růžička des. 2009 [p, red label] // Necrophila / (Chrysosilpha) / formosa / (Laporte, 1832) [p] \bigcirc [hw] / Jan Růžička det. 200 [p] 8 [hw]".

Additional material examined. See Appendix 1.

Diagnostic description. Body length 13.0–17.0 mm (15.5 mm in the lectotype of *S. formosa*), maximum body width 7.0–9.0 mm (8.5 mm in the lectotype). Head with red brown to yellow gular region. Anterior emargination of labrum narrow, deep (Fig. 30). Pronotum orange with four large spots arranged in quadrate position medially on the disc, posterior pair is larger, or as large as the anterior pair (Figs. 1–2, 25). Proventrite orange, with metallic green only posteriorly on medial projection (Fig. 33). Elytra metallic green or rarely metallic blue (Figs. 1–2).



FIGURES 1–2. Habitus dorsally of *Necrophila* (*Chrysosilpha*) *formosa* (Laporte) (1, ♂, JRUC; 2, ♀, JRUC, both Payakumbuh, Harau Valley, Sumatra, Indonesia). Scale bar 5 mm.

Male. Apex of elytron regularly rounded, without apical denticle (Fig. 1). Genital segment with elongate ventrite 9; spiculum gastrale robust, as long as ventrite 9 (Fig. 8). Length of aedeagus 3.0 mm, median lobe robust, widely rounded apically (Fig. 7). Parameres robust (Fig. 7). Basal portion of aedeagus robust (Fig. 7).

Female. Apex of elytron slightly elongate, straight in posteroapical part, without apical denticle (Fig. 2). Tergum 10 elongate, with posterior margin wide (Fig. 9). Tergum 9 narrow and oval in ventral view (Fig. 10). Stylus distinctly longer than apex of coxite in ventral view (Fig. 10).

Notes on synonymy. The differences between *N*. (*C*.) *formosa* and *N*. (*C*.) *chloroptera*, described by Portevin (1921, 1926) (proportions and shape of pronotum; relative size of anterior and posterior black spots on pronotum; punctation of elytra), fall within intraspecific variability, with gradual transitions. Originally, Laporte (1840) only refers to Laporte (1832) and repeats the same diagnosis without mentioning any differences between the two taxa.

Consequently, Silpha chloroptera Laporte, 1840 is treated here as a junior subjective synonym of Silpha (Oiceoptoma) formosa Laporte, 1832.

Portevin (1921) described *Chrysosilpha chloroptera* var. *magnifica* based only on colour variation of elytra (bluish, with golden shine vs. metallic green). He did not specify a type locality (Portevin 1921: 538). The same is repeated by Portevin (1926: 106–107). The same colour variability is noticed here in a series of specimens from Malaysia: Cameron Highlands, without any clear geographic separation of the two colour forms. Consequently, *Chrysosilpha chloroptera* var. *magnifica* Portevin, 1921 is treated here as a junior subjective synonym of *Silpha* (*Oiceoptoma*) *formosa* Laporte, 1832.

Ecology. Scarce locality data indicate necrophagous and saprophagous association with decaying tropical vegetation and traps baited with decaying fish. Two specimens from North Indonesia (Sumatera Utara Province, 25 km N of Sipirok) were found in a secondary forest, in inflorescence of *Amorphophallus gigas* Teijsm & Binnend (Araceae) (name of the plant provided on locality label is its junior synonym, *A. brooksii* Alderw.). Inflorescence of this plant species is known to produce trimethylamine, mimicking the odour of decaying fish (Kakishima *et al.* 2011). Miyake (1987) mentioned possible predaceous behaviour of *N. (C.) formosa* in a tree flower in lowland forest at Batu 19 (Cameron Highlands, Perak, Malaysia). Specimen data indicate that adults are active year round (but there are no vouchers from December), with most specimens collected during January–May and October (Table 2). The species has been collected from sea level to 2500 m in Sumatera Barat, Indonesia.

TA	BLE	2.	Seasonal	activity	of N .	(C.)	formosa	(Laporte).
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month	1	2	3	4	5	6	7	8	9	10	11	12
number of specimens	19	7	12	4	15	9	9	4	7	24	6	0

Published records on distribution. Tonkin [northern Vietnam, misidentified or mislabelled specimen(s) (?), not located in MNHN] (Portevin 1920); Cochinchina [southern Vietnam] (Portevin 1920); "Sunda Islands" (Portevin 1920); Malaysia: Malacca [= Melaka] (Hatch 1928); Malaysia: Selangor [Ulu Gombak (Univ. Malaya Field Studies Centre) [ca. 03°13'N 101°43'E], 15.vi.2006, Y. Katayama leg. (e-mail to M. Nishikawa from Hiroshi Ikeda)] (Ikeda *et al.* 2008b).

Distribution. Widely distributed species (Fig. 40), known from Laos, Vietnam, Thailand, Malaysia (Kuala Lumpur, Johor, Kedah, Perak, Pahang, Melaka, Selangor and a single imprecise record from Sabah), Indonesia (Aceh, Riau, Sumatera Barat, Sumatera Selatan, Sumatera Utara, Bangka-Belitung Islands, Banten, Jawa Barat, Jawa Tengah, Jawa Timur and Bali).

Necrophila (Chrysosilpha) renatae (Portevin, 1920), comb. nov.

(Figs. 3-4, 11-14, 24, 26, 34, 35, 38-40)

Eusilpha (Calosilpha) Renatae Portevin, 1920b: 505 (description, type locality "Iles Malaises") *Chrysosilpha Renatae*: Portevin 1921: 538 (new combination, supplementary description) *Chrysosilpha Renatae*: Portevin 1926: 107, 151 (key, catalogue) *Silpha (Chrysosilpha) Renatae*: Hatch 1928: 112 (new combination, catalogue)

Type material examined. Holotype \bigcirc (MNHN), labelled (Fig. 24): "Iles / Malaises [hw, yellow label] // TYPE [p, red characters] // MUSEUM PARIS / Coll. A. Grouvelle 1915 [p] // HOLOTYPE / Eusilpha (Calosilpha) / renatae Portevin, 1920 / (label added by / Jan Růžička, 2009) [p, red label] // Necrophila (Chrysosilpha) / renatae / (Portevin, 1920) [p] \bigcirc [hw] / Jan Růžička det. 200 [p] 8 [hw]".

Additional material examined. See Appendix 1.

Diagnostic description. Body length 16.0–18.5 mm (17.0 mm in the holotype), maximum body width 8.0–9.5 mm (9.0 mm in the holotype). Head with metallic blue gular region. Anterior emargination of labrum wide, shallow (as on Fig. 31). Pronotum metallic dark blue, only anterolateral portion orange (Figs. 3–4). Proventrite metallic blue or green (Fig. 34). Elytra metallic blue or green (Figs. 3–4).

Male. Apex of elytron obliquely truncate, with distinct apical denticle (Fig. 3). Genital segment with wider ventrite 9; spiculum gastrale slender, distinctly shorter than ventrite 9 (Fig. 12). Length of aedeagus 2.8 mm,



FIGURES 3–6. Habitus dorsally of *Necrophila* (*Chrysosilpha*) *renatae* (Portevin) (3, 3, JRUC; 4, 9, BMNH, both Dumoga-Bone Nat. Park, banks of Tumpah River, Sulawesi) and *N*. (*C*.) *viridis* (Motschulsky) (5, 3, JRUC; 6, 9, JRUC, both Mindanao, Sebu Lake, Philippines). Scale bar 5 mm.



FIGURES 7–18. Genitalia of *Necrophila* (*Chrysosilpha*) formosa (Laporte) (7–8, , JRUC, and 9–10, 9, JRUC, both Payakumbuh, Harau Valley, Sumatra, Indonesia), *N.* (*C.*) renatae (Portevin) (11–12, , JRUC, and 13–14, 9, BMNH, both Dumoga-Bone Nat. Park, banks of Tumpah River, Sulawesi) and *N.* (*C.*) viridis (Motschulsky) (15–16, , JRUC, and 17–18, , JRUC, both Mindanao, Sebu Lake, Philippines), setae omitted. Aedeagus ventrally (7, 11, 15); 3 genital segment ventrally (8, 12, 16); genital segment dorsally (9, 13, 17) and ventrally (10, 14, 18). Abbreviations: c—coxite, s—stylus, sg—spiculum gastrale, t9—tergum 9, t10— tergum 10, v9—ventrite 9.

median lobe slender, with apex narrowed to a slender tip (Fig. 11). Parameres slender (Fig. 11). Basal portion of aedeagus slender (Fig. 11).

Female. Apex of elytron wide, elongate, distinctly sinuate in posteroapical part, with distinct apical denticle (Fig. 4), only rarely is denticle only very minute. Tergum 10 transverse, with posterior margin narrow (Fig. 13). Tergum 9 wide and subquadrate in ventral view (Fig. 14). Stylus distinctly longer than apex of coxite (Fig. 14).

Ecology. Scarce locality data indicate necrophagous association with dead rat and traps baited with decaying fish and excrements, and also attraction to light trap. Specimen data indicate that adults are active all year round (with no vouchers only from February and July), with most specimens collected in January, April and December (Table 3). The species has been collected at altitudes between 200–1700 m.

TABLE 3. Seasonal activity of N. (C.) renatae (Portevin).

month	1	2	3	4	5	6	7	8	9	10	11	12
number of specimens	15	0	2	31	1	1	0	5	4	8	2	20

Published records on distribution. Celèbes [= Sulawesi] (Portevin 1926), Celebes [= Sulawesi] (Hatch 1928).

Distribution. Endemic to Indonesia: Sulawesi, known from Sulawesi Selatan, Sulawesi Tengah, Sulawesi Tenggara and Sulawesi Utara provinces (Fig. 40).

Necrophila (Chrysosilpha) viridis (Motschulsky, 1861), comb. nov.

(Figs. 5-6, 15-18, 22-23, 27, 28, 31, 36, 37, 40)

Oiceoptoma viridis Motschulsky, 1861a: 628 (description, type locality "Philippinen") Oiceoptoma viridis: Motschulsky 1870: 349 (redescription) Silpha viridis: Schultze 1915: 29 (new combination, catalogue) Calosilpha viridis: Portevin 1920a: 398 (new combination) Calosilpha viridis: Portevin 1920b: 505 (diagnosis) Chrysosilpha viridis: Portevin 1921: 538 (new combination, supplementary description) Chrysosilpha viridis: Portevin 1926: 107-108, 151 (key, catalogue) Silpha (Chrysosilpha) viridis: Hatch 1928: 112 (new combination, catalogue) Oiceoptoma (Thanatophilus) viridis: Arnett 1950: 63 (new combination, redescription) Silpha coelestis Dohrn, 1875: 81 (description, type locality "Insulae Philippinae") Chrysosilpha coelestis: Portevin 1921: 538 (new combination, supplementary description) Chrysosilpha caelestis [sic]: Portevin 1926: 108 (key) Chrysosilpha coelestis: Portevin 1926: 151 (catalogue) Silpha (Chrysosilpha) coelestis: Hatch 1928: 112 (new combination, catalogue) Oiceoptoma (Thanatophilus) coelestis: Arnett 1950: 65 (new combination, junior subjective synonym of Oiceoptoma viridis) Silpha superba Kraatz, 1876: 374 (description, type locality "Luzon") Silpha superba: Arrow 1909: 63 (junior subjective synonym of Silpha coelestis)

Type material examined. Holotype ♂ of *Oiceoptoma viridis* (head and abdomen missing) (ZMUM), labelled (Fig. 22): "Type [hw] // [small yellow triangular label = sign for Oriental region] // 239. [hw] // Oiceoptoma / viridis / Motsch / Ins. Philip [hw, Motschulsky's ms, yellow label] // [red label] // HOLOTYPE / Oiceoptoma viridis / Motschulsky, 1861 / (label added by / Jan Růžička, 2009) [p, red label] // Necrophila (Chrysosilpha) / viridis / (Motschulsky, 1861) [p] ♂ [hw] // Jan Růžička det. 2009 [p]".

Holotype 3° of *Silpha superba* (antennae missing except for right antennomeres 1 and 2; dissected, aedeagus labelled on small card pinned with specimen) (SDEI), labelled (Fig. 23): "Is. Luzon. [hw] // Silpha / superba / 1877 m. [hw, Kraatz's ms] // Eusilpha / coelestis Dohrn [hw] / det. G. Portevin [p] 1876 [hw] // Holotypus [hw, red label] // coll. DEI / Eberswalde [p] // CHRYSOSILPHA / viridis Motschulsky / det. Barries 2001 [p] // coll. SDEI / (Müncheberg) / general coll. [p] // HOLOTYPE / Silpha superba / Kraatz, 1876 / (label added by / Jan Růžička, 2009) [p, red label] // Necrophila (Chrysosilpha) / viridis / (Motschulsky, 1861) [p] 3° [hw] / Jan Růžička det. 200 [p] 9 [hw]".

Additional material examined. See Appendix 1.



FIGURES 19–24. Habitus dorsally and labels of lectotype \bigcirc of *Silpha formosa* Laporte (19, MNHN), lectotype \bigcirc of *Silpha chloroptera* Laporte (20, MNHN), lectotype \bigcirc of *Chrysosilpha chloroptera* ver. *magnifica* Portevin (21, MNHN), holotype \eth of *Oiceoptoma viridis* Motschulsky (22, ZMUM), holotype \eth of *Silpha superba* Kraatz (23, SDEI) and holotype \bigcirc of *Eusilpha renatae* Portevin (24, MNHN). Scale bars 5 mm.



FIGURES 25–28. Pronotum dorsally of *Necrophila (Chrysosilpha) formosa* (Laporte) (25, 3, JRUC, Payakumbuh, Harau Valley, Sumatra, Indonesia), *N. (C.) renatae* (Portevin) (26, 3, JRUC, Dumoga-Bone Nat. Park, banks of Tumpah River, Sulawesi) and *N. (C.) viridis* (Motschulsky) (27, 3, JRUC, Mindanao, Sebu Lake, Philippines; 28, 9, WBAC, Luzon, Aurora, Philippines). Scale bars 1 mm.

Diagnostic description. Body length 12.0–18.5 mm (14.0 mm combined length of pronotum and elytra [head missing] in the holotype), maximum body width 6.5–10.0 mm (8.0 mm in the holotype). Head with metallic blue gular region, sometimes lighter brown laterally in subteneral specimens. Anterior emargination of labrum wide, shallow (Fig. 31). Pronotum metallic blue to green, with orange spot anterolaterally, which is elongated laterally in a narrow strip reaching the posterior corner of pronotum, and with narrow orange line along posterolateral margin (Figs. 5–6, 27), only very rarely (a single specimen in the material examined) completely reduced posterolaterally (Fig. 28). Proventrite metallic blue or green. Elytra metallic blue.



FIGURES 29–39. Morphological details of *Necrophila*. Head dorsally of *Necrophila* (*Necrophila*) *americana* (Linnaeus) (29, \mathcal{O} , JRUC, Point Pelee, Canada), *N.* (*Chrysosilpha*) *formosa* (Laporte) (30, \mathcal{O} , JRUC, Payakumbuh, Harau Valley, Sumatra, Indonesia) and *N.* (*C.*) *viridis* (Motschulsky) (31, \mathcal{O} , JRUC, Mindanao, Sebu Lake, Philippines). Detail of anterior part of pronotum, punctation in dorsal view, *N.* (*N.*) *americana* (32, \mathcal{O} , JRUC, Point Pelee, Canada). Proventrite ventrally of *N.* (*C.*) *formosa* (33, \mathcal{O} , JRUC, Payakumbuh, Harau Valley, Sumatra, Indonesia) and *N.* (*C.*) *renatae* (Portevin) (34, \mathcal{O} , JRUC, Dumoga-Bone Nat. Park, banks of Tumpah River, Sulawesi). Left antenna in dorsal view of *N.* (*C.*) *renatae* (35, same specimen). Detail of male metatarsus in dorsal view of *N.* (*C.*) *viridis* (36, \mathcal{O} , JRUC, Mindanao, Sebu Lake, Philippines). Apex of male elytron ventrally of *N.* (*C.*) *viridis* (37, same specimen). Abdomen ventrally of *N.* (*C.*) *renatae* (39, same specimen). Scale bars 1 mm (0.25 mm for 32, 0.5 mm for 39).



FIGURE 40. Known distribution of *Necrophila (Chrysosilpha) formosa* (Laporte) (thick margins for state records only), *N.* (*C.) renatae* (Portevin) and *N.* (*C.) viridis* (Motschulsky) in Oriental region.

Male. Apex of elytron truncate almost at right angle, with small apical denticle (Fig. 5). Genital segment with very narrow, elongate ventrite 9; spiculum gastrale slender, only slightly shorter than ventrite 9 (Fig. 16). Length of aedeagus 3.0 mm, median lobe very slender, with rounded apex (Fig. 15). Parameres very slender (Fig. 15). Basal portion of aedeagus slender, more robust only medially (Fig. 15).

Female. Apex of elytron slender, elongate, only slightly sinuate in posteroapical part, with distinct apical denticle (Fig. 6). Tergum 10 wide, with posterior margin wide, regularly rounded (Fig. 17). Tergum 9 narrow and oval in ventral view (Fig. 18). Stylus only slightly longer than apex of coxite (Fig. 18).

Notes on synonymy. Differences between *N*. (*C*.) *viridis* and *N*. (*C*.) *coelestis*, described by Portevin (1926) (fine or absent punctation on pronotal disc; minor shade differences in colouration of pronotum and elytra; different extension of orange spot laterally on pronotum etc.), fall within intraspecific variability, with gradual transitions. We confirm here the opinion of Arnett (1950), who stated synonymy of the two taxa.

The type specimens of beetle species described by Carl August Dorn (1806–1892) were deposited in the former Museum für Naturkunde in Stettin (Horn *et al.* 1990). Later, the collection was transferred to the Polish Academy of Sciences, Institute of Zoology, Warszawa (MZPW) (Newton & Thayer 2005). However, according to Dominika Mierzwa, curator of MZPW (e-mail of 30 April 2010), type material of *Silpha coelestis* was not found in its collections.

Ecology. Scarce locality data indicate necrophagous association with dead fish and bird carrions, and presence of numerous lepidopteran scales on specimen from Mindanao (from RMNH) also indicates attraction to a light

trap. Specimen data indicate that adults are active all year round (with no vouchers from February), with most specimens collected in January, April–June and August–September (Table 4). The species has been collected from sea level to 2130 m in Mindanao Is., Philippines.

TABLE 4. Seasonal activity of N. (C.) viridis (Motschulsky).

month	1	2	3	4	5	6	7	8	9	10	11	12
number of specimens	33	0	3	11	19	25	3	17	18	3	3	8

Published records on distribution. Philippines: Manila (Motschulsky 1870); Mindoro Is.: Mt. Halkon (Schultze 1915), Mindanao Is.: nine localities, Cebu Is.: Bugo [= Bogo, ca. 11°03'N 124°00'E] (Arnett 1950).

Distribution. Endemic to Philippines, known from Luzon, Mindoro, Leyte, Cebu and Mindanao Islands (Fig. 40).

Phylogeny

The implicit enumeration run of TNT resulted in a single most parsimonious tree with a length of 27 steps (CI = 0.88, RI = 0.72) (Fig. 41). The analysis supports the subgenus *Chrysosilpha* as monophyletic (with bootstrap of 85), based on derived states of 6 characters, unique for this clade (1-1: frons in dorsal view with distinctly indicated fovea; 7-1: punctation of scutellum fine to very fine; 9-1: colour of elytra in dorsal view metallic blue or green; 10-1: elytral epipleural ridge, lateral elevation in dorsal view weakly elevated; 12-1: elytral epipleura, ventral view in males with a prominent, oblique crest posteriorly).



FIGURE 41. Single most parsimonious tree (L = 27; CI = 0.88; RI = 0.72) obtained from implicit enumeration analysis. Only unambiguously optimized evolutionary events are mapped. Character numbers are given above, character states below. Solid rectangles indicate unique character state transformations, open rectangles indicate homoplastic character state transformations. Numbers below branches indicate standard bootstrap (1000 replicates).

Within *Chrysosilpha*, *N*. (*C*.) *formosa* was recovered as sister to a clade of *N*. (*C*.) *renatae* and *N*. (*C*.) *viridis* (with bootstrap of 85) (Fig. 40). *N*. (*C*.) *formosa* is characterized as a distinct lineage, based on derived states of 5 characters, 4 of which are unique for this clade (5-2: colour of pronotum in dorsal view orange with four large spots; 6-2: proventrite colouration orange, with metallic blue only on medial projection; 14-0: apex of elytron, simple in female; 17-1: male aedeagus, lateral part of basal portion in ventral view robust).

The clade of N. (C.) renatae and N. (C.) viridis was supported based on derived states of 5 characters, 4 of which are unique for this clade (2-1: anterior emargination of labrum wide, shallow; 5-3: colour of pronotum in dorsal view metallic blue or green-blue with anterolateral or lateral part orange; 6-1: proventrite colouration metallic blue or green; 13-1: apex of elytron truncate in male).

Geometric morphometrics

The relative warps (RWs) for male and female elytral apexes of the three *Necrophila* (*Chrysosilpha*) species were calculated and plotted on an axis system. The first RW axis, representing 66.06% of shape variability, indicated a significant sexual dimorphism in the elytral shape between the sexes when compared together. The second RW axis explained 20.75% of variability (Fig. 42). As a consequence of this high sexual dimorphism, each sex was tested separately to further perceive the shape differences between the taxa. Among the male groups, the first RW axis accounted for 55.19% of the total variance whereas the second axis accounted for only 15.12% (Fig. 43). On the other hand, a higher 57.63% of variability explained by the first RW axis and 19.55% by the second axis was observed between the females of the species (Fig. 44).

In general, the elytral shape of female *Chrysosilpha* can be seen as more pear-shaped than those of the males. In addition, N. (C.) *viridis* and N. (C.) *renatae* in both sexes have a small denticle on the subapical part of the elytral apex.

The scatter plot of the two first RWs for male *Chrysosilpha* displayed overlap between all groups (Fig. 43), but it was greater between N. (*C*.) *renatae* and N. (*C*.) *viridis*. In N. (*C*.) *formosa* and N. (*C*.) *renatae* the overlap was minimal, caused only by two specimens of N. (*C*.) *viridis* (Fig. 43). The thin-plate spline (TPS) transformation grids indicated the shape change of the elytral apex on the RW axes from widely rounded with no apical denticle in N. (*C*.) *formosa* to obliquely truncate with a small denticle in N. (*C*.) *renatae* to less prominent and in extreme almost rectangular with a larger denticle in N. (*C*.) *viridis* (Fig. 43, inset grids).



FIGURE 42. Scatter plot of the first two relative warp scores for both female (left) and male (right) elytral apex of *Necrophila* (*Chrysosilpha*). Symbols used: *N.* (*C.*) *formosa* (Laporte)—empty circle for male, plus for female specimens; *N.* (*C.*) *renatae* (Portein)—filled triangle for male, filled rhomboid for female specimens; *N.* (*C.*) *viridis* (Motschulsky)—star for male, empty triangle for female specimens.



FIGURE 43. Relative warps scatter plot of the elytral apex of male *Necrophila* (*Chrysosilpha*). Insets represent variation in thin-plate spline (TPS) transformation grids of elytral apex for selected specimens; elytral apex is oriented to left.

The first two female RWs also indicated an overall overlap of all groups, although it was slighter between N. (*C*.) *formosa* and N. (*C*.) *viridis* (Fig. 44). The deformation grids illustrate the elytral shape change from straighter, slightly elongate in N. (*C*.) *formosa* towards a more elongate and distinctly sinuate in the apical part, with smaller denticle in N. (*C*.) *renatae* to a more protruding shape, only slightly sinuate in the apical part, with a larger denticle in N. (*C*.) *viridis* (Fig. 44, inset grids).

Body shape diversity between the studied taxa was reinforced by MANOVA, where the female groups demonstrated significant shape variability (F = 59.39; Wilk's $\lambda = 0.01131$; d.f. = 30/212; p < 0.0009). Similarly, male groups revealed great shape differences (F = 42.78; Wilk's $\lambda = 0.01849$; d.f. = 30/202; p < 0.0001).

To acquire a clearer view as to the separation of the studied groups, two individual canonical variate analyses for males and females were conducted on the first 15 axes of the RW scores matrix that cover 99.24% of the shape variation between the males and 99.59% between the females. In both cases, the first two canonical axes clearly indicated separation of the taxa into three distinct groups (Figs. 45). There is no overlap between the groups and there was a 100% correct assignment of each specimen to its given group mean. Moreover, in analyses of both sexes, N. (C.) formosa appeared to be more separate from both N. (C.) viridis and N. (C.) renatae (Figs. 45). The

latter two were closer to each other, which suggests that they are more similar in shape but yet form separate species. These results are consistent with the cladistic analysis.



FIGURE 44. Relative warps scatter plot of the elytral apex of female *Necrophila* (*Chrysosilpha*). Insets represent variation in thin-plate spline (TPS) transformation grids of elytral apex for selected specimens; elytral apex is oriented to left.

Discussion

Zoogeography. Wallace's line had already been proposed already in the 19th century as a zoogeographical border between the Oriental and Australian biogeographic regions (Wallace 1860). Historical separation of these regions is also supported also by recent reconstruction of plate tectonics evolution (Hall 2002). Pleistocene glaciations also caused the sea level to be lowered by 100 m, which exposed a considerable area of continental shelf and allowed land bridges to form between biogeographical regions (Voris 2000). Consequently, at least some beetle groups repeatedly crossed this line, as documented, for example, by Balke *et al.* (2009) and Bocak & Yagi (2009).

Molecular sequences are available only for one of the three *Necrophila* (*Chrysosilpha*) species, *N*. (*C*.) *formosa* (Ikeda *et al.* 2008; cited as *C. chloroptera*). The phylogenetic hypothesis presented above is based only on adult morphological characters, and *N*. (*C*.) *formosa* is considered a sister to a clade containing *N*. (*C*.) *renatae* and *N*. (*C*.) *viridis*.

It seems possible that *Chrysosilpha* colonized the Sundaland region (the present islands on the Sunda Shelf associated with southeastern Asia) from mainland Asia, because other Old World subgenera of *Necrophila* (including *Eusilpha*, considered a sister to *Calosilpha* and *Chrysosilpha* by Ikeda *et al.* [2008]) are known only from continental Asia, Taiwan and Japan (Portevin 1926). *Necrophila* (*C.*) *formosa* is known also from several records from continental Asia (Laos, Vietnam and Thailand), and the easternmost known record of this species is from Bali, west of Wallace's line. The single record of *N.* (*C.*) *formosa* from Borneo is from "Sabah" (without more details), possibly based on mislabelled specimens.



FIGURE 45. Canonical variate analysis (CVA) of male (above) and female (below) elytral apex of Necrophila (Chrysosilpha).

The subgenus probably crossed Wallace's line, while the other two species are much more local: *N*. (*C*.) *renatae* is restricted to Sulawesi and *N*. (*C*.) *viridis* to Philippines. This clade is habitually uniform, with general morphological similarity supported by four synapomorphies. In the traditional zoogeographical view, however, the Philippines is considered a part of Sundaland while Sulawesi as a part of Wallacea (the present islands associated with the northern margin of the Australian Plate) (Simpson 1977). The observed pattern more supports the concept of Huxley's line, whereby the fauna of the Philippines is excluded from the Oriental region (Huxley 1868). Close relationships between arthropod populations or species distributed over the Philippines and Sulawesi were also confirmed by de Bruyn *et al.* (2004), and Kubecek *et al.* (2011).

Sikes *et al.* (2006) postulated a similar invasion scenario for carrion beetles of the *Nicrophorus nepalensis* species group (Coleoptera: Silphidae: Nicrophorinae) from continental Asia through the Malay Archipelago to Sumatra, Java and Bali, reaching New Guinea and the Solomon Islands, with a higher species diversity in this clade (eight species).

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- APPENDIX 1. List of additional examined (non-type) material of Necrophila (Chrysosilpha).

Necrophila (Chrysosilpha) formosa (Laporte, 1832) (226 specimens)

Laos: "Laos", without more detailed locality, without date [but before 1905], ex coll. Sharp, $1 \stackrel{\circ}{\downarrow}$ (BMNH);

- **Vietnam:** Cochinchine [centroid ca. 11°00'N 107°00'E], without date [but before 1915] and collector's name, ex coll. A. Grouvelle, 1 \bigcirc (MNHN); Cochinchina, without date [but before 1915], Collection Mniszech, ex coll. A. Grouvelle, 2 $\bigcirc \bigcirc$ (MNHN);
- Thailand: "Lower Siam", Trong [= Trang province], Khow Sai Dow [not located], 1000 ft [ca. 300 m], i.–ii.1899, without collector's name [probably W.L. Abbott leg.], 1 ♂ (NMNH); "Lower Siam", Trong [= Trang province, centroid ca. 07°30'N 099°40'E], without date, W.L. Abbott leg., 1 ♂ (NMNH); Chiang Mai province: Chiang Mai [ca. 18°47'N 098°59'E], v.1988, G. Minet leg., 1 ♀ (NHMB);
- **Malaysia:** <u>Federal Territory of Kuala Lumpur</u>: Kuala Lumpur [ca. 03°09'N 101°42'E], v.1950, Army Scrub Typhus Unit, 1 ♀ (NMNH); same locality, 1950, Army Scrub Typhus Unit, 1 ♂, 2 ♀♀ (NMNH); same locality, vii.1976, without collector's name, decaying fish bait, 1 ♀ (SMNS);

Johor: road Kota Tingi – Mersing, 20 km N Kota Tingi [ca. 01°53'N 103°54'E], 1.–14.i.2008, M. Pejcha leg., 1 $\stackrel{\circ}{\downarrow}$ (JSSC);

Kedah: "N. Kedah", Talan Sintok [ca. 06°26'N 100°31'E], iv.-vii.1938, A. J. Slater leg., ex mass of trop. vegetation, 2 33

(BMNH);

- Perak: Taiping [ca. 04°51'N 100°43'E], vi.1977, Wong leg., 1 ♂, 1 ♀ (SMNS); same locality, ix.1984, without collector's name, 1 ♂ (SMNS); without more detailed locality, without date [but before 1905], Doherty leg., ex coll. Fry, 1 ♂ (BMNH); Presqu'ile de Malacca [= Malay Peninsula], Tapah [ca. 04°11'N 101°15'E], 1900, O. B. Cerruti leg., 1 ♀ (MNHN); Cameron Highlands, iii.–v.1985, Wong leg., 2 ♀♀ (SMNS); Cameron Highlands, 19 miles [= Batu 19, SW of Ringlet, ca. 04°22.2'N 101°20.0'E], 3.i.1983, Y. Gunji leg., 1 ♂ (NSMT); same locality, iii.1988, G. Hangay leg., 1 ♂ (HNHM); same locality, 600–660 m, 10.–18.v.2011, fish and prawn-baited pitfall trap, P. Šípek & D. Vondráček leg., 1 ♀ (JRUC);
- Pahang: Benom Mountains, 15 km E Kampong Dong, 03°53'N 102°01'E, 300–1000 m, 24.iii.–15.iv.1998, Dembický & Pacholátko leg., 2 ♀♀ (JSCC); Cameron Highlands [ca. 04°28'N 101°26'E], v.1986, without collector's name, 1 ♂, 1 ♀ (NSMT); same locality, v.1986, without collector's name, 1 spec. (MNIC); same locality, iii.2002, without collector's name, 1 spec. (MNIC); same locality, iii.2002, without collector's name, 1 ♂ (TFUC); same locality, vii.2007, without collector's name, 1 ♂ (TFUC); Cameron Highlands, Tana Rata [= Tanah Rata, ca. 04°27'N 101°22'E], early v.1988, W.T. Fatt leg., 1 spec. (MNIC); Kinta Highlands [= Genting Highlands, ca. 03°25'N 101°47'E], 300 m, 9.i.2005, 1 spec. (MNIC); Bukit Kutu [ca. 03°28'N 101°57'E], 3300 ft. [ca. 1000 m], iv.1929, A. R. Sanderson leg., 2 ♂♂ (BMNH); Pekan [ca. 03°29'N 103°23'E], x.1918, G.D. Allen leg., 2 ♂♂, 6 ♀♀ (OUMNH); Gunung Benom Mt., 20 km NE Raub, Lata Jarom [ca. 03°54'N 102°00'E], 350–550 m, 19.–22.ii.1995, M. Štrba & R. Hergovits leg., 1 ♀ (JSSC);
- <u>Melaka</u>: Malacca [= Melaka, ca. 02°12'N 102°15'E], without date [but before 1917] and collector's name, ex coll. A. Grouvelle, 1 \bigcirc (MNHN); Malacca, without date [but before 1922] and collector's name, ex coll. L. Bedel, 1 \bigcirc (MNHN); Malacca [= Melaka], without date [but before 1922], I. Z. Kannegieter leg., ex coll. L. Bedel, 1 \bigcirc (MNHN); Malacca, without date, W. Doherty leg., ex coll. R. Oberthur, 2 \bigcirc 1 \bigcirc (MNHN); Malacca, without date and collector's name, ex Mus. Westerm., 1 \bigcirc (ZMUC);

Selangor: Kepong [ca. 03°10'N 101°34'E], x.1949, in forest, Army Scrub Typhus Unit, 1 ♂, 2 ♀♀ (NMNH); Ulu, Gombak Station [ca. 03°13'N 101°43'E], 300 m, 17.–22.xi.1988, W. Rohe leg., 4 ♂♂, 2 ♀♀ (SMNS);

- Sabah:
 [centroid ca. 05°15'N 117°00'E], without more detailed locality, ii.2004, without collector's name, 1 ♂, 1 ♀ (TFUC);

 Indonesia:
 Aceh:
 Alastal [= Alas valley], N Kotatjane [= Kutacane], 27.i.1974, Diehl leg., 1 ♂ (SMNS); 30 km NW Kutacane

 [= Kotacane, ca. 03°41'N 097°38'E], Alastal [= Alas valley], Ketambe [ca. 03°43'N 097°37'E], 21–25.i.1995, C. Zorn leg., 1 ♂, 2 ♀♀ (FMNH, JRUC); same locality, 400 m, 7.–19.x.1991, W. Barries leg., 4 ♂♂, 6 ♀♀ (FMNH, JRUC, JSCC, WBAC); Alas valley, 320 m, viii.1972, J. Krikken leg., multistratal evergreen forest, 1 ♀ (RMNH); Deli, Kuala Simpang [ca. 04°16'N 098°03'E], v.1953, A. Sollaart leg., lowland forest, 1 ♀ (RMNH);
- Bengkulu: Mt. Lalangie [= Lalangi, ca. 03°21'S 101°48'E], 3500 ft. [ca. 1068 m], vii.1923. C. J. Brooks leg., No. 14985, 1 ♀ (BMNH); same data, No. 14976, 1 ♂ (BMNH); same data, No. 14902, 1 ♂ (BMNH); same data, No. 14987, 1 ♂ (BMNH); Riau: road to Dumai, Duri env. [ca. 01°34'N 101°22'E], i.2007, 0–100 m, S. Jakl leg., 1 ♀ (JSSC);
- Sumatera Barat:Pajakombo [= Payakumbuh, ca. 00°13'S 100°37'E], without date [but before 1915] and collector's name, exSumatera Barat:Pajakombo [= Payakumbuh, ca. 00°13'S 100°37'E], without date [but before 1915] and collector's name, excoll. A. Grouvelle, 1 ♀ (MNHN); Payakumbuh, i.1991, without collector's name, 2 ♂♂, 2 ♀♀ (JSCC); Pajakombo,without date, H. Romper leg., 1 ♀ (RMNH); Payakumbuh, Harau valley, i.1991, R. Dunda leg., 2 ♂♂, 2 ♀♀ (JRUC,JSCC); same locality, 10.–20.ii.1991, S. Jakl leg., 1 ♂ (JSSC); same locality, vii.1992, without collector's name, 1 ♀(WBAC); same locality, 700 m, x.2004, without collector's name, 1 ♂ (JSCC); Payakumbuh, Harau Mt., 1000 m, 5.–10.ii.1991, S. Jakl leg., 1 ♂ (JRUC); ca. 35 km N of Payakumbuh, Landai vill. env., Mt. Sanggul [not located], 1250–1400m, vii.2007, S. Jakl leg., 1 ♀ (LKLC); Gunung Teleman [= Gunung Ophir, also known as Gunung Talakmau, ca. 00°05'N099°59'E], v.1917, E.J. v. Jacobson leg., 1 ♀ (RMNH); Fort de Kock [= Bukittinggi, ca. 00°18'S 100°21'E], 920 m, 1924,E. Jacobson leg., 1 ♂ (ZMAN); jungle between Loeboe and Loeboe-Taka [not located], 6.–8.vi.1907, O. John leg., 1 ♀(ZMAS); Singgalang [=Gunung Singgalang, ca. 00°23'S 100°20'E], iii.1991, without collector's name, 1 ♀ (JSCC); Anaivalley [ca. 00°30'S 100°20'E], 400 m, x.1995, S. Jakl leg., 1 ♀ (JSCC); Westnhelling, Bochit Barisan [= BarisanMountains], Korintji [= Gunung Kerintji Mt., ca. 01°42'S 101°15'E], 2500 m, x.1921, F. J. Pratt leg., 1 ♀ (ZMAN); KandsAmpat [= Kandang Ampat], Pad. Benedenl., i.–iv. 1888, without collector's name, ex coll. A. Grouvelle 1915, 1 ♂, 3 ♀♀(MNHN);
- Sumatera Selatan: Palambong [= Palembang, ca. 02°59'S 104°45'E], without date and collector's name, ex coll. A. Grouvelle 1915, 1 \bigcirc (MNHN); Palembang, without date and collector's name, ex coll. A. Grouvelle 1917, 4 \bigcirc \bigcirc , 3 \bigcirc \bigcirc (MNHN); Palembang, without date, M. Knappert leg., 1 \bigcirc , 2 \bigcirc (RMNH); Rég. de Benkoeien, Tandjong Sakti [= Tandjungsakti, ca. 04°10'S 103°04'E], 1935, Mme M.E. Walsh leg., ex coll. R. Oberthur, 1 \bigcirc , 1 \bigcirc (MNHN);
- Sumatera Utara: Brastagi [= Berastagi, ca. 03°11'N 098°31'E, ca. 1400 m], v.1987, without collector's name, vi.1987, 5 spec. (MNIC); same locality, without collector's name, vi.1987, 5 spec. (MNIC); same locality, without collector's name, 2 ♂♂, 1 ♀ (NSMT); "Insula Nias", without date, J.D. Pasteur leg., 1 ♂, 1 ♀ (RMNH); Nias Is., "N. Nias", Hili Madjedja [= Hili Maziaya, ca. 01°24'N 097°24'E], 4di trim. [18]95, I. Z. Kannegieter leg., ex coll. A. Grouvelle, 3 ♀♀ (MNHN); Tapanuli district, 25 km N Sipirok [ca. 01°48'N 099°15'E], 28.viii.1993, W. Hetterscheid leg., secondary forest, in flower of *Amorphophallus brooksii*, 1 ♂, 1 ♀ (RMNH); Sipirok [ca. 01°36'N 099°15'E], without date, A.L. v. Hasselt leg., 1 ♂ (RMNH); Padang Sidempoean [= Padang Sidempuan, ca. 01°23'N 099°16'E], without date [probably between 1888– 1891], J.D. Pasteur leg., 1 ♂, 1 ♀ (RMNH); Tandjong Morawa [= Tandjung Morawa, ca. 03°31'N 098°48'E], without date and collector's name, 1 ♀ (SDEI); Médan, Env. de Dolok-Baros [= Dolok-Baros caoutchouc- en koffie cultuur Maatschappij, 12 miles from Arnhemia railway station, ca. 03°28'N 098°36'E], 2e semestre 1905, without collector's name, ex coll. A. Grouvelle, 1 ♀ (MNHN); Dolok Bartong [ca. 02°30'N 099°33'E], Oeloe Koewoloe [= Ulu Kuwolu], 350 m, without date, K.E. Keil leg., 2 ♂♂, 5 ♀♀ (RMNH); Soekaranda [= Sukaranda, ca. 03°34'N 098°17'E], i.1894, Dohrn leg., 1 ♂ (HNHM); Liangagas [ca. 03°16'N 098°13'E], without date, Dohrn leg., 1 ♂ (SMTD); Tandjong Kasso [= Tanjungkasau, ca. 03°17'N 099°17'E], without date, Trescher leg., 1 ♀ (SDEI); Tebing-Tinggi [ca. 03°19'N 099°10'E],

without date and collector's name, $1 \stackrel{\circ}{\circ} (ZSM)$; Tebing-Tiggi [= Tebing Tinggi], 10.vi.1962, E. Diehl leg., ex coll. Hangay, $1 \stackrel{\circ}{\circ} (HNHM)$; same locality, 30.vii.1962, E. Diehl leg., ex coll. Hangay, $1 \stackrel{\circ}{\circ} (HNHM)$; "Sumatra's O. K." [= Oostkust], Bedagei int. [= Sungai Bedagei, ca 03°30'N 099°12'E], ±600 ft [= 183 m], 2^{de} Sem [18]89, I. Z. Kannegieter leg., $3 \stackrel{\circ}{\circ} \stackrel{\circ}{\circ} (SMTD)$; same data, ex coll. G. Kraatz, $1 \stackrel{\circ}{\circ} , 1 \stackrel{\circ}{\circ} (SDEI)$; same data, ex coll. L. Bedel, $1 \stackrel{\circ}{\circ} (MNHN)$; ex coll. A. Grouvelle, $2 \stackrel{\circ}{\circ} \stackrel{\circ}{\circ} (MNHN)$; same data, ex coll. I. Lhost, $1 \stackrel{\circ}{\circ} (IRSNB)$;

Bangka-Belitung Islands: Banka [=Bangka Island, ca. 02°15'S 106°00'E], v.1905, Hagen leg., 1 (ZSM);

Jawa, Banten: Gedeh [= Tanjung Gedeh, ca. 05°55'S 106°03'E], without date, ex coll. Oberthur, "I. G. 18293", 1 $\stackrel{\circ}{_+}$ (IRSNB);

- <u>Jawa Barat</u>: Buitenzorg [= Bogor, ca. 06°35'S 106°47'E], vi.–viii.1931, W.C. van Heurn leg., 1 \bigcirc (RMNH); Preanger Regentschappen [= Priangan Highlands, ca. 07°15'S 107°30'E], 1899, ex coll. M. Bartels, 1 \Diamond , 1 \bigcirc (ZMAN);
- Jawa Tengah: Pelaboean Ratoe [ca. 06°37'S 111°31'E], without date, Bryan & Palmer leg., 1 ♂ (NMNH); Noesa Kembangan [= Nusa Kambangan Is., ca. 07°43'S 108°54'E], without date [but before 1899], C. Auriv.[illius] leg., 1 ♂ (NHRS); Radja Mandala [= Mandala, ca. 07°21'S 108°53'E], 1899, Lédru leg., ex coll. R. Oberthur, 1 ♀ (MNHN);

<u>Jawa Timur</u>: G. Bantjar [= Bancar, ca. $06^{\circ}46$ 'S 111°45'E], viii.1931, Handschin leg., 1 $\stackrel{\circ}{+}$ (NHMB);

<u>Bali</u>: Negara [ca. 08°21'S 114°37'E], 400 m, i.2005, without collector's name, $2 \stackrel{\bigcirc}{\downarrow} \stackrel{\bigcirc}{\downarrow} (JSSC)$;

Imprecise or unlocated records. "India or., Tetra[spilota?]", without date and collector's name, 1 👌 (ZMAN); "Nepal" [mislabelled specimen], without date and collector's name, CNHM 1955 Eduard Knirsch Palaearctic collection, 1 🖒 (FMNH); "Malay Pen"[insula], without date [but before 1915] and collector's name, ex coll. A. Grouvelle, $1 \stackrel{\bigcirc}{\rightarrow}$ (MNHN); "N Borneo", without date and collector's name, 2656 and 2659, 1 ♂, 1 ♀ (SDEI); "Borneo", without date [but before 1917], v. Rom leg., $1 \Leftrightarrow$ (ZMAN); Borneo, Sumatra, 1873, without collector's name, $1 \diamondsuit$, $1 \Leftrightarrow$ (MNHN); "Sumatra occid.", Loeboe Banghoe [not located], without date, J. Henzel leg., $2 \sqrt[3]{?}$, $1 \neq$ (RMNH); "Sumatra", without date and collector's name, 1 ♀ (NHMB); "Sumatra", without date and collector's name, 1 ♂ (JSSC); "Sumatra", without date, ex coll. Melly, 1 ♂ (MHNG); "Sumatra", without date, ex coll. Staudinger, 1 ♂ (MHNG); "Sumatra", without date, Muller leg., 1 ♂, 1 ♀ (RMNH); "Sumatra", without date, ex coll. Tunkl, $1 \stackrel{\bigcirc}{_{\sim}}$ (HNHM); "Sumatra", without date, ex coll. H. Nessel, $1 \stackrel{\bigcirc}{_{\sim}}$ (ZSM); "Sumatra", without date, ex Mus. Leyden, S.[ilpha] splendida Dehaan [unpublished manuscript name], 1 ♂ (ZMUC); "Sumatra", 1864, without collector's name, 1 $\stackrel{\circ}{\downarrow}$ (OUMNH); "Sumatra", 1866, Wallace leg., 1 $\stackrel{\circ}{\triangleleft}$, 3 $\stackrel{\circ}{\downarrow} \stackrel{\circ}{\downarrow}$ (OUMNH); "Sumatra", 1879, Higgins leg., ex coll. G. Lewis, 1 👌 (BMNH); "Sumatra", without date [but before 1879], without collector's name, 1 \circlearrowleft (BMNH); "Sumatra", without date [but before 1905], Wallace leg., ex coll. Fry, 2 $\bigcirc \bigcirc$ (BMNH); "Sumatra", 1920, ex coll. H. J. Carter, 1 3 (BMNH); "Sumatra", without date [but probably between 1921–1929], H. Bandat leg., 2 ♂♂ (HNHM); "Coyrtsug, Achonnsgit" [illeg.], 1918, without collector's name, 1 ♀ (ZMAN); "Java", without date and collector's name, ex Mus. Westerm., $1 \stackrel{\circ}{\downarrow} (ZMUC)$; "Java", without date, ex coll. Melly, $1 \stackrel{\circ}{\downarrow} (MHNG)$; no locality data, ex coll. A. Grouvelle 1915, 1 $\stackrel{?}{\circ}$ (MNHN); "Patria ignota", without date and collector's name, 1 $\stackrel{\bigcirc}{\circ}$ (ZMAN);

Necrophila (Chrysosilpha) renatae (Portevin, 1920) (104 specimens)

Indonesia: Sulawesi Selatan: Puncak Palopo [ca. 02°57'S 120°05'E], i.2009, T. Ikeda leg., 9 spec. (MNIC);

- Sulawesi Tengah: Toli-Toli [Tolitoli, ca. 01°03'N 120°49'E], xi.–xii.1895, H. Fruhstorfer leg., $1 \stackrel{\bigcirc}{_{\sim}}$ (SMTD); same data, ex coll. A. Grouvelle 1915, 1 ♂, 1 ♀ (MNHN); Sopu [ca. 01°11'S 120°07'E], 1000–1500 m, 1979, E. de Vogel leg., 1 ♀ (RMNH); Lore Lindu National Park, near Dongi-Dongi shelter, 01°15'S 120°20'E, ca. 975 m, 4.xii.1985, C. van Achterberg leg., 1 ♂, 1 ♀ (RMNH); Lore Lindu National Park, Dongi Dongi shelter, 940 m, 4.–8.xii.1985, multistratal evergreen forest, fish traps, J. Krikken leg. (pw52), 2 33, 3 99 (RMNH); Lore Lindu National Park, Dongi Dongi (garage), 950 m, 4.-9.xii.1985, multistratal evergreen forest, clearing, fish traps, J. Krikken leg. (pw55c), 1 9 (RMNH); Lore Lindu National Park, Sopu River forest [ca. 01°13'S 120°11'E], 940 m, 7.–9.xii.1985, multistratal evergreen forest, human excrement traps, J. Krikken leg. (pw52), 1 👌 (RMNH); Lore Lindu National Park, Marena forest near river [ca. 01°32'S 120°00'E], 600 m, 14.–17.xii.1985, multistratal evergreen forest, fish traps, J. Krikken leg. (pw64b), 5 ♂♂, 4 ♀♀ (RMNH); Lore Lindu National Park, Marena shelter [ca. 01°32'S 120°01'E], 600 m, 14.–17.xii.1985, second-growth forest, J. Krikken leg. (pw65b), 5 33, 1 9 (RMNH); Donggala district, Lore Lindu National Park, Kamaroro env. [= Kamarora, ca. 01°20'S 119°57'E], 13.-18.iv.1994, M. Hiermeier leg., 1 3 (ZSM); Palolo near Palu [ca. 01°38'S 119°53'E], 23., 25. and 26.iv.1985, K. Maruyama leg., 17 spec. (MNIC); same locality, ii.1996, without collector's name, 1 d (WBAC); same locality, vi.1996, native collector leg., 1 Q (TFUC); same locality, 17.ix.2001, without collector's name, 2 spec. (MNIC); Palu, Paolo [=Palolo], without date and collector's name, 1 3 (TFUC); Palu, Palolo, Kamarora trail to waterfall, 700 m, 23.–27.viii.1997, A. Riedel leg., 1 ♀ (JSSC); Palolo near Palu, Puncak Dingin [not located], 23.iv.1985, K. Maruyama leg., 9 spec. (MNIC); 15–25 km S Pendolo, Mayoa env. [ca. 02°08'S 120°43'E], 7.–10.iv.1999, Bečvář & Zábranský leg., 1 \bigcirc (WBAC); Palopo, x.1999, without collector's name, 1 \Diamond , 2 $\bigcirc \bigcirc$ (JSSC); Puncak Palopo pass [not located], viii.2004, 600–1000 m, 1 3, 2 9 9 (JSSC); Puncak Palopo, iv.2007, without collector's name, 1 9 (LKLC); Totop camp along Batui river, SW Luwuk, 01°09'S 122°31.5'E, 120 m, 21.x.1989, J. P. Duffels leg., lowland rainforest, understorey canopy, at light, 1 3, 1 9 (ZMAN); Sarapi [not located], 14.viii.2009, Y. Kondo leg., 1 spec. (MNIC); Palu region, Tawaeli – Tomboli road (km 34) [ca. 00°42'S 119°57'E], 500 m, 20.–22.xii.1985, degraded multistratal evergreen forest, fish trap, J. Krikken leg. (pw 69b), $1 \stackrel{\bigcirc}{\downarrow}$ (RMNH);
- Sulawesi Tenggara: Kolaka, Sanggona Base Camp [ca. 03°45'S 121°40'E], 200 m, 13.–17.x.1989, multistratal evergreen forest, fish trap, Krikken & Van der Blom leg. (sw 06b), 2 ♀♀ (RMNH); same locality, 10.–21.x.1989, second-growth forest, hand collected, Krikken & Van der Blom leg. (sw 08), 1 ♂ (RMNH);
- Sulawesi Utara: Tondano [= Danau Tondano lake, ca. 01°13'N 124°53'E], 1866, Wallace leg., 1 ♂ (OUMNH); NE Kotamobagu, Modoinding env. [ca. 00°47'N 124°24'E], 19.iv.1992, M. Jäch leg., 1 ♀ (NHMW); Popayato [= Papayato, ca. 00°30'N 121°28'E], 1.v.1985, K. Maruyama leg., 1 spec. (MNIC); Dumoga-Bone Nat. Park [ca. 00°30'N 123°25'E], 10.iii.1985, without collector's name, Project Wallace, pitfall trap, meat bait, 1 ♀ (BMNH); Dumoga-Bone Nat. Park,

banks of Tumpah river [ca. 00°34'N 123°54'E], 250 m, 22.i.1985, without collector's name, Project Wallace, dead rat, $1 \stackrel{\circ}{\triangleleft}$, $4 \stackrel{\circ}{\supsetneq} \stackrel{\circ}{\downarrow}$ (BMNH, JSCC); same locality, 16.i.1986, P.M. Hammond leg., $1 \stackrel{\circ}{\triangleleft}$ (JRUC); Dumoga-Bone Nat. Park, along S. Dosinggolan, E slopes of Bone mountains, 860 m, 19.ix.1981, at light, primary forest with dense undergrowth on slope of narrow river valley, W.F. Rodenburg leg., $2 \stackrel{\circ}{\supsetneq} (RMNH)$; Dumoga-Bone Nat. Park, S. Moinakom, S slopes of Kablia range, 530 m, 16.iii.1982, in small clearing in lightly disturbed primary forest, near stream, W.F. Rodenburg leg., $1 \stackrel{\circ}{\dashv} (RMNH)$;

Imprecise or unlocated records. "Celebes", Ile-Ile [not located], 1700 m, 15.xi.1930, G. Heinrich leg., $1 \stackrel{\circ}{\circ}$, $1 \stackrel{\circ}{\circ}$ (BMNH); same locality, 500 m, xii.1930, G. Heinrich leg., $1 \stackrel{\circ}{\circ}$, $1 \stackrel{\circ}{\circ}$ (BMNH); "Sulawesi, 5192", without date, Grunwald leg., $1 \stackrel{\circ}{\circ}$ (SMNS); "Celebes", without date and collector's name, $1 \stackrel{\circ}{\circ}$ (JRUC);

Necrophila (Chrysosilpha) viridis Motschulsky, 1861 (181 specimens)

- **Philippines:** Luzon Is.: Manille [= Manila, ca. 14°35'N 120°59'E], without date [but before 1917] and collector's name, ex coll. A. Grouvelle, 1 \bigcirc (MNHN); same locality, without date [but before 1917], collection Mniszech, ex coll. A. Grouvelle, 1 \bigcirc (MNHN); Montalban [ca. 14°43'N 121°06'E], without date [but before 1942], Lohr leg., 1 \bigcirc (coll. W. Schultze, SMTD); [Tayabas province / Nueva Vizcaya province], Casiguran, Mt. Alzapan [not located], vi.1925, McGregor leg., 1 \bigcirc , 1 \bigcirc (NMNH); Rizal province, Mt. Irid [ca. 14°47'N 121°20'E], xii.1926, F. Rivera leg., 1 \bigcirc , 2 \bigcirc (NMNH); same locality, without collector's name, 4 \bigcirc \bigcirc , 4 \bigcirc (coll. W. Schultze, SMTD); "N Luzon", Ilocos Norte province, Cabugao [ca. 17°47'N 120°27'E], i.1984, 1 \bigcirc (NSMT); Ilocos Norte province, Mt. Palimlim [not located], without date [but before 1942], without collector's name, 2 \bigcirc \bigcirc \bigcirc (2 \bigcirc (Coll. W. Schultze, SMTD); Sierra Madre Mts., Aurora province [centroid ca. 15°53'N 121°33'E], iv.2007, native collector leg., 5 \bigcirc \bigcirc , 4 \bigcirc (WBAC); Ilocos Sur province, Quirino [ca. 17.16°N 120.67°E, 317 m], v.2008, without collector's name, 2 spec. (MNIC); same locality, viii.2008, without collector's name, 2 spec. (MNIC); Shiera madore [sic!], Quirino, viii.2008, native collector leg., 1 \bigcirc (TFUC); "N Luzon", Mountain province, vi.1990, without collector's name, 1 \bigcirc (MNHN); without more precise locality, without date [but before 1917] and collector's name, ex coll. A. Grouvelle, 1 \bigcirc (MNHN);
- <u>Mindoro Is.</u>: Mt. Halkon [= Mt. Halcon, ca. 13°15.8'N 120°59.7'E], 600 m, 7.vii.2007, without collector's name, 1 $\stackrel{\circ}{\supset}$ (TFUC); same locality, ix.2008, without collector's name, 1 $\stackrel{\circ}{\hookrightarrow}$ (TFUC);

<u>Cebu Is.</u>: Bugo [= Bogo, ca. 11°03'N 124°00'E], without date and collector's name, $1 \stackrel{\bigcirc}{_{+}}$ (NMNH);

- Mindanao Is.: Bukidnon province, Mt. Banquon [not located], vi.2003, without collector's name, $1 \stackrel{\bigcirc}{_{\sim}} (JSSC)$; Davao [ca. 07°04'N 125°36'E], without date [but before 1915], Dr. Platen leg., ex coll. A. Grouvelle, 1 \mathcal{Q} (MNHN); Davao [del Norte] province, E slope of Mt. McKinley, 3000 ft [ca. 915 m] [not located], 29.viii.1946, CNHM-Philippine Zool. Exped. (1946– 47), F.G. Werner leg., by stream, 1 d (FNMH); Davao [del Norte] province, E slope of Mt. McKinley, 6500 ft [ca. 1980 m], 1.–12.ix.1946, CNHM-Philippine Zool. Exped. (1946–47), H. Hoogstraal leg., bird meat on ground, mossy forest, 3 33, 2 99 (FMNH, NMNH); Davao [del Norte] province, E slope of Mt. McKinley, 3150 ft [ca. 960 m], 3.ix.1946, CNHM-Philippine Zool. Exped. (1946–47), H. Hoogstraal leg., original forest, $2 \stackrel{\circ}{\circ} \stackrel{\circ}{\circ}$, $1 \stackrel{\circ}{\circ}$ (FNMH); Davao [del Norte] province, E slope of Mt. McKinley, 6400 ft [ca. 1950 m], 10.ix.1946, CNHM-Philippine Zool. Exped. (1946-47), H. Hoogstraal leg., from meat-baited trap, $1 \stackrel{\circ}{\triangleleft}, 1 \stackrel{\circ}{\subsetneq}$ (FNMH); South Cotabato province, Mt. Parker [ca. 06°07'N 124°54'E], 2000-3000 m, 8.xii.1984, without collector's name, fish trap, 1 spec. (MNIC); South Cotabato province, Mt. Parker, Lake Maugham, 1700 m, 6.iv.1986, R.A. Müller leg., light trap, 1 3 (RMNH); Mt. Apo, vi.-vii. [without year], E.A. Mearns leg., 9 3 3, 6 9 9 (NMNH); Mt. Apo, Mainit River [ca. 06°40'N 125°17'E], 10.ix.1930, C.F. Clagg leg., ex coll. F. Psota, 6 33, 599 (FMNH, SMNS); Mt. Apo, Seliban River, 6000 ft [ca. 1830 m], 29.viii.1930, C.F. Clagg leg., sweeping, ex coll. F. Psota, 1 \bigcirc , 1 \bigcirc (FMNH); same locality, 31.viii.1930, C.F. Clagg leg., ex coll. F. Psota, 5 \bigcirc \bigcirc , 4 \bigcirc (FMNH); Mt. Apo, Galog River, 6000 ft [ca. 1830 m], 5.ix.1930, C.F. Clagg leg., ex coll. F. Psota, $1 \stackrel{\circ}{\circ}, 1 \stackrel{\circ}{\subsetneq}$ (FMNH); Mt. Apo, Baroring River, 9.xi.1930, 7000 ft [ca. 2130 m], C.F. Clagg leg., ex coll. F. Psota, 4 ♂♂, 1 ♀ (FMNH); Davao [del Norte] province, E slope of Mt. Apo, Mainit [hot springs, ca. 07°02'N 125°14'E], 4300 ft [ca. 1310 m], xi.1946, CNHM-Philippine Zool. Exped. (1946–47), H. Hoogstraal leg., 1 \bigcirc (FMNH); Davao [del Norte] province, E slope of Mt. Apo, Baclayan [= Baclayan camp, not located], 6500 ft [ca. 1980 m], 16.xi.1946, CNHM-Philippine Zool. Exped. (1946-47), H. Hoogstraal leg., 1 ♂ (NMNH); Mt. Apo [ca. 06°59'N 125°16'E], without date, Crampton leg., ex coll. A. Newton & M. Thayer ex MCZ, $1 \triangleleft$, $1 \subsetneq$ (FMNH); same locality, vi.1982, without collector's name, 3 spec. (MNIC); same locality, iii.1983, without collector's name, 1 \bigcirc (NSMT); same locality, ix.1994, without collector's name, 5 spec. (MNIC); same locality, v.2004, without collector's name, 12 spec. (MNIC); same locality, v.2004, native collector leg., $1 \stackrel{\circ}{\circ}, 1 \stackrel{\circ}{\circ}$ (TFUC); same locality, iii.2006, without collector's name, 1 spec. (MNIC); same locality, v.2007, without collector's name, 3 spec. (MNIC); Northern Mindanao prov., Bukidnon distr., Mt. Kitanglad [= Mt. Katanglad, ca. 08°06'N 124°55'E], iv.1987, without collector's name, $1 \stackrel{\bigcirc}{_{\sim}}$ (NSMT); same locality, vii.1993, without collector's name, 1 spec. (MNIC); S. Cotabato province [= Region XII], Sebu Lake, $06^{\circ}13$ 'N 124°42'E, 700 m, 1.–7.xii.1997, P. Lays leg., $2 \Im \Im$ (IRSNB); same locality, 1.–15.i.1998, P. Lays leg., 15 $\Im \Im$, 12 $\Im \Im$ (IRSNB); same data, 3 $\Im \Im$, 3 $\Im \Im$ (JRUC); Sultan Kudarat province, Mt. Syniop [ca. 06°28'N 124°03'E], x.2000, 3 spec. (MNIC); Compostela Valley province, Monkyo [= Monkayo, ca. 07°49'N 126°02'E], 27.vii.2007, without collector's name, 1 spec. (MNIC); Mt. Hilonghilong [ca. 09.09°N 125.70°E], 1200 m, 3.viii.1978, A. Yamamoto leg., 1 3, 1 2 (NSMT); without more precise locality, without date [but before 1917] and collector's name, ex coll. A. Grouvelle, $1 \stackrel{\bigcirc}{\downarrow}$ (MNHN);
- **Imprecise or unlocated records.** "Philipp. Is.", 237, without date [but before 1863], Bowring leg., 1 \circ (BMNH); "Philippin", without date, ex coll. H. Nessel, 1 \circ (ZSM); "Philippines, Mindanao", vi.2004, without collector's name, 2 $\circ \circ$, 1 \circ (JSSC); "Camp I" [without precise locality], 1450 m, 5.xii.1951, Tilg, Braestrup leg., 1 \circ , 1 \circ (ZMUC); no data, ex coll. A. Grouvelle, 1 \circ , 1 \circ (MNHN).